

Cleptoparasitic Behavior and Immatures of the Bee

Melecta duodecimmaculata

(Apoidea: Apidae: Melectini)

Appendix: Tribal Descriptions of the Anthophorini and Melectini Based on Their Mature Larvae

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ABSTRACT

This study describes the nesting biology of the cleptoparasitic bee *Melecta duodecimmaculata* (Rossi), which attacked a nesting site of *Anthophora* (s. str.) *melanognatha* Cockerell (Apidae: Anthophorini) in Beijing, China. In addition, we provide an account of its first and last larval instars and information concerning ovarian statistics and mature oocytes. Comparisons are made with previous accounts of the cleptoparasitic behavior and anatomy of immature stages of other Melectini. We also explore the phylogenetic relationship of the Melectini with the Anthophorini and with other cleptoparasitic Apinae (especially the Ericrocidini) in light of this information. Appended are accounts of larval anatomy of the Melectini and Anthophorini at the tribal level based on taxa whose mature larvae were available or had been described.

INTRODUCTION

We report for the first time on the nesting biology and cleptoparasitic behavior of *Melecta* (s. str.) *duodecimmaculata* (Rossi) and describe its first and last larval instars and mature oocyte. This information is integrated with what is already known about other Melectini to

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provide a more complete understanding of tribal biology. This species attacked nests of *Anthophora* (s. str.) *melanognatha* Cockerell (Apoidea: Apidae: Anthophorini) at Hu Yu, Beijing, China (N 40° 16.537' E 116° 08.764', elev. 184 m). We then discuss the phylogenetic relationships of the Melectini with other Apidae, especially the Anthophorini and Ericrocidini, as revealed by their biology and immature stages. Appended we include tribal descriptions of the Anthophorini and Melectini based on mature larvae of all species whose larvae are available including *A. melanognatha* and *M. duodecimmaculata*.

METHODS

Preserved mature larvae were prepared for study as follows: The larval head was separated from the body, and both were cleared in an aqueous solution of sodium hydroxide. After being washed in water they were transferred to 70%–75% ethanol and stained with Chlorazol Black E, which imparted a bluish hue to reveal otherwise undetectable, slightly sclerotized areas on postcephalic integument. The specimen was then washed in ethanol, and submerged in glycerin on a well slide for examination, illustration, and storage. Specimens (mature oocytes, the first instar) to be examined with a Hitachi S-4700 scanning electron microscope (SEM) were critical-point dried, mounted on stubs, and then coated with gold/palladium.

Mandibular anatomy plays a significant role in distinguishing melectine taxa. In descriptions, the long axis of the right mandible is assumed to be horizontal, so that the upper (or top) surface is dorsal and the lower surface is ventral. In depicting inner views, the adductor apodeme base was carefully aligned over that of the abductor apodeme, and in dorsal and ventral views, bases of the two apodemes were at the same level. In diagrams, frontal views of head show distribution of internal head ridges on the right side and approximate distributions of spicules and sensilla on the left.

To determine the index of foramen to head width of mature larvae, the maximum transverse width of the foramen is divided by the maximum transverse head width. This is a measure of the degree of constriction of the posterior edge of the head capsule relative to the lateral expansion of the parietals.

BIOLOGY

Although previously not studied, the nesting site of *Anthophora melanognatha* at Hu Yu had been known for more than 25 years to biologists who often collected in the area. In the past the site seemed larger than now. L.D. and Feng Yuan led J.G.R. and John S. Ascher to it on May 19, 2011, when we excavated several nests and collected a small series of adults and a few adults of its cleptoparasite, *Melecta duodecimmaculata*. The site was a somewhat sloping surface recessed under a low overhang, at most 1 m high, created by a large rock outcrop on the east-facing side of a valley (figs. 1, 2). The surface was only marginally exposed to the sun and was sheltered from rain. On June 13, L.D. returned to the site and collected a large number of cells from which 139 live host larvae and 6 live *M. duodecimmaculata* larvae (5 defecating and the other large and about



FIGURES 1, 2. Nesting site of *Anthophora melanognatha* at Hu Yu, Beijing Province, China. **1.** Rock overhang with nesting site in shadow under it to the left of the figures. **2.** Close-up of site with J.G.R. and L.D. excavating nests, entrances of which were mostly in the shadow. (Photographs of figs. 1 and 2 by J.S. Ascher.) FIGURES 3–5. Inner surface of cell closures of *Anthophora melanognatha* showing egg insertion holes of *Melecta duodecimmaculata* (arrows). FIGURES 6, 7. Feeding larvae of *Melecta duodecimmaculata*, **6.** Intermediate instar. **7.** Last larval instar.

to defecate) were retrieved. Additionally, a first instar and five perhaps second or third cleptoparasitic instars were also collected, but no pupae or cocoons were encountered.

The paucity of *Anthophora melanognatha* adults flying about the site and the large number of partly and fully grown larvae indicated that the main active period at the site had passed, and the low ratio of cleptoparasite larvae to host larvae seemed to imply a low parasitism rate. Further, we did not recover any live eggs of either host or parasite. Indeed, several years earlier L.D. had seen large numbers of females and a few males of *A. melanognatha* at the site between April 10 and 20 as well as some female (but no male) *Melecta duodecimmactulata*. Although not observed during our visit in May, *A. (Melea) plagiata* Illiger nested here with *A. melanognatha* in April of previous years but in fewer numbers. L.D. observed *M. duodecimmactulata* visited their nests as well.

When opening cells of *Anthophora melanognatha*, we inspected the internal cell surfaces, especially their closures, for evidence of *Melecta* insertion holes and eggs, for we knew that melectine bees introduce their eggs into closed host cells by making small holes in the closure ends through which they introduced their eggs (Semichon, 1904; Torchio and Youssef, 1968; Rozen, 1969a; Thorp, 1969; Westrich, 1989 [and references therein]; Rozen and Özbek, 2005). We were unable to observe the actual egg-laying behavior of *M. duodecimmactulata*, but Semichon (1904) related that a female *Melecta* (s. str.) *albifrons* (Forster) (as *M. armata* Panzer) dug into a nest of the host *Anthophora fulvitaris* Brullé (as *A. personata* Illiger), deposited an egg through a somewhat moist cell cap, and then backfilled the nest tunnel, a process that took only 5 min. We wonder whether a moist, presumably soft cell cap might be important, allowing easy penetration by the cleptoparasite, and if so, whether it might be a clue as to how female parasites distinguish nests in the right stage for parasitizing from older nests in which provisions had been partly or completely consumed. Torchio and Youssef (1968) related that a female of *Melecta* (s. str.) *pacifica* Cresson entered a nest of its anthophorine host one hour after the host female closed it, and “during the subsequent five-hour period, the parasite parasitized one cell and replugged the nest.” Thus their observation supports the possibility that only fresh cells are attacked, but the amount of time involved seems quite variable. Thorp (1969) found that female *M.* (s. str.) *separata callura* (Cockerell) spent 45–105 min in host nests and took about 10 min to reseal the burrow but did not determine when cells had been constructed relative to parasitization. On the other hand, Rozen and Özbek (2003) in studying the egg-laying habits of *Xeromelecta (Melectomorpha) californica* (Cresson) tentatively concluded that females could oviposit in cells in which the closure had dried. They also thought that, while females used their mandibles to dig through cell caps, melectine females used the apex of their metasomas to punch through the closures because of the small diameters of the holes revealed on the inner surface of cell closures of a great many species.

We discovered seven cells of *Anthophora melanognatha* with 1–3 egg insertion holes of *Melecta duodecimmactulata* (figs. 3–5) mostly centrally positioned on the cap, although one cell had one of its two holes located at the periphery (fig. 4). After ovipositing, parasite females had filled most of the holes with fine sand mixed with a presumably hardening liquid, and in some cases the fill material projected a short distance into the cell lumen below (fig. 5). Some shriveled, empty parasite chorions were attached to the inner closure surfaces, an indication that Melectini usually, if not invariably, attach their eggs to the inner closure surface or to the upper wall of the

vertical cell by one or both ends (Semichon, 1904; Malyshev, 1928: fig. 7; Torchio and Youssef, 1968; Thorp, 1969; Torchio and Trostle, 1986; Rozen and Özbek, 2005).³ Evidence of a liquid adhesive in the form of a slightly shiny area on the surface near a hole existed in several cases. Torchio and Youssef (1968) hypothesized that the first instar of *Zacosmia maculata* Cresson nesting in a cell tilted about 30° from horizontal may tear through the anterior end of its egg and crawl over the vacated chorion to the cell closure. Subsequently Torchio and Trostle (1986) provided an insightful account of late embryogenesis and eclosion of *Xeromelecta californica* whereby the emerging larva slowly descends from its chorion and usually crawls over and down the cell wall “because host cells are oriented at various angles away from vertical.” Although many parasitized cells of *A. melanognatha* had been attacked several times (judged by numbers of egg insertion holes), we never found more than one surviving cleptoparasite in a cell, indicating that newly eclosed parasites quickly eliminate all competition for provisions.

Young larvae of *Melecta duodecimmaculata* were encountered partly submerged while feeding on the liquefied provisions (fig. 6). Later provisions became more solid and older larvae curled around them (fig. 7). Because we recovered only defecating and predefecating larvae, we were unable to confirm whether *Melecta duodecimmaculata* spins a cocoon, although it seems likely since *M. separata callura*, *Zacosmia maculata*, and *Xeromelecta californica* are reported to do so (Linsley and MacSwain, 1942; Porter, 1951; Torchio and Youssef, 1968; Thorp, 1969; Torchio and Trostle, 1986). Of all melectine genera, larvae of only *Thyreus* and *Thyreomelecta*⁴ presumably do not spin cocoons (Cardale, 1968; Rozen, 1969a, 2000),⁵ although Torchio and Trostle (1986) noted a situation in which the first generation of a bivoltine population of *X. californica* infrequently spun cocoons.

OVARIAN STATISTICS AND EGG/MATURE OOCYTE

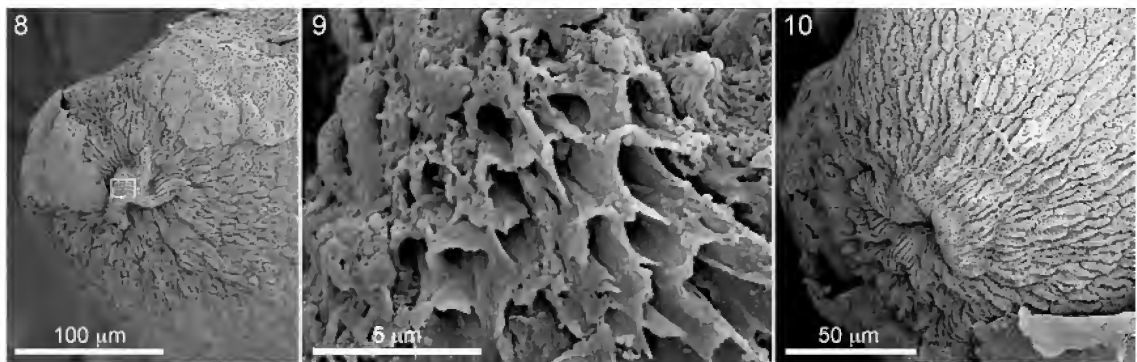
Figures 8–10

From a single dissected female of *Melecta duodecimmaculata* with an ovarian formula of 4:4, we retrieved four mature oocytes. Table 1 provides all accumulated ovarian statistics for melectine bees studied so far. These indicate that *M. duodecimmaculata* is a typical melectine with an egg index of 0.57, placing it in the *small* category of Iwata and Sakagami's (1966) system of classifying bee eggs relative to the body size of females. By contrast, cleptoparasitic Apidae that deposit eggs in open cells (i.e., cells in which the host female has yet to lay her egg) tend to have eggs classified as *dwarf*, the smallest category.

3Rozen (1969) did not find eggs of *Thyreus lieftincki* cemented to the inner surface of the host's cell closure but allowed that they may have been dislodged by vibrations caused by nest excavation.

4 The pupa of *Thyreomelecta kirghisia* Rightmyer and Engel (as *Thyreus* sp.) was described by Rozen (2000), and as stated in the paper it was taken from the brood chamber with its cast larval skin and without a cocoon (brood chamber, skin, and pupa preserved in the collection of the AMNH). On this basis we conclude neither *Thyreus* nor *Thyreomelecta* spins a cocoon.

5 A single postdefecating larva recognized and described by Rozen (1969) as *Thyreus* sp. was recovered by him among a series of larval *Amegilla salteri* collected by C.D. Michener in Australia (Michener, 1960). Likely the collector overlooked it because its body form strongly resembled that of the host. Had it been wrapped in a cocoon, it would have been immediately recognizable since *A. salteri*, like all anthophorines, does not produce a cocoon.



FIGURES 8–10. SEM micrographs of mature oocytes of *Melecta duodecimmaculata*. 8. Anterior end of oocyte still partly enclosed by follicular tissue, showing micropyle (identified by rectangle). 9. Close-up of micropyle. 10. Anterior end of another oocyte (with micropylar area invaginated, not visible) showing radiating chorionic ornamentation.

TABLE 1. Comparative Data on Number and Sizes of Mature Oocytes /Eggs and Number of Ovarioles of Melectine Bees. Numbers in first three columns are means if more than one specimen was examined.

Taxon	Egg index	Total no. mature oocytes	Mature oocytes per ovariole	No. ovarioles	No. specimens	Source of data
<i>Melecta albifrons</i>	0.59	3	0.38	4:4	3	Rozen and Özbek, 2003
<i>M. duodecimmaculata</i>	0.57	4	0.5	4:4	1	Current study
<i>Thyreomelecta kirghisia</i> Rightmyer & Engel	0.68	4	0.5	4:4	3	Rozen and Özbek, 2003
<i>Thyreus decorus</i> (Smith) ^a	0.85	3.5	0.438	4:4	2	Iwata, 1955; Iwata and Sakagami, 1966
<i>Thyreus lieftincki</i> ^b	0.82-0.84	–	–	–	–	Rozen and Özbek, 2003
<i>T. ramosus</i> (Lepeletier) ^b	0.67	–	–	–	2	Rozen and Özbek, 2005
<i>Xeromelecta californica</i>	0.59	5.33	0.67	4:4	3	Rozen and Özbek, 2003
<i>Zacosmia maculata</i> Cockerell	0.74	6	0.75	4:4	1	Alexander and Rozen, 1987

^aAs *Thyreus japonicus* (Fries).

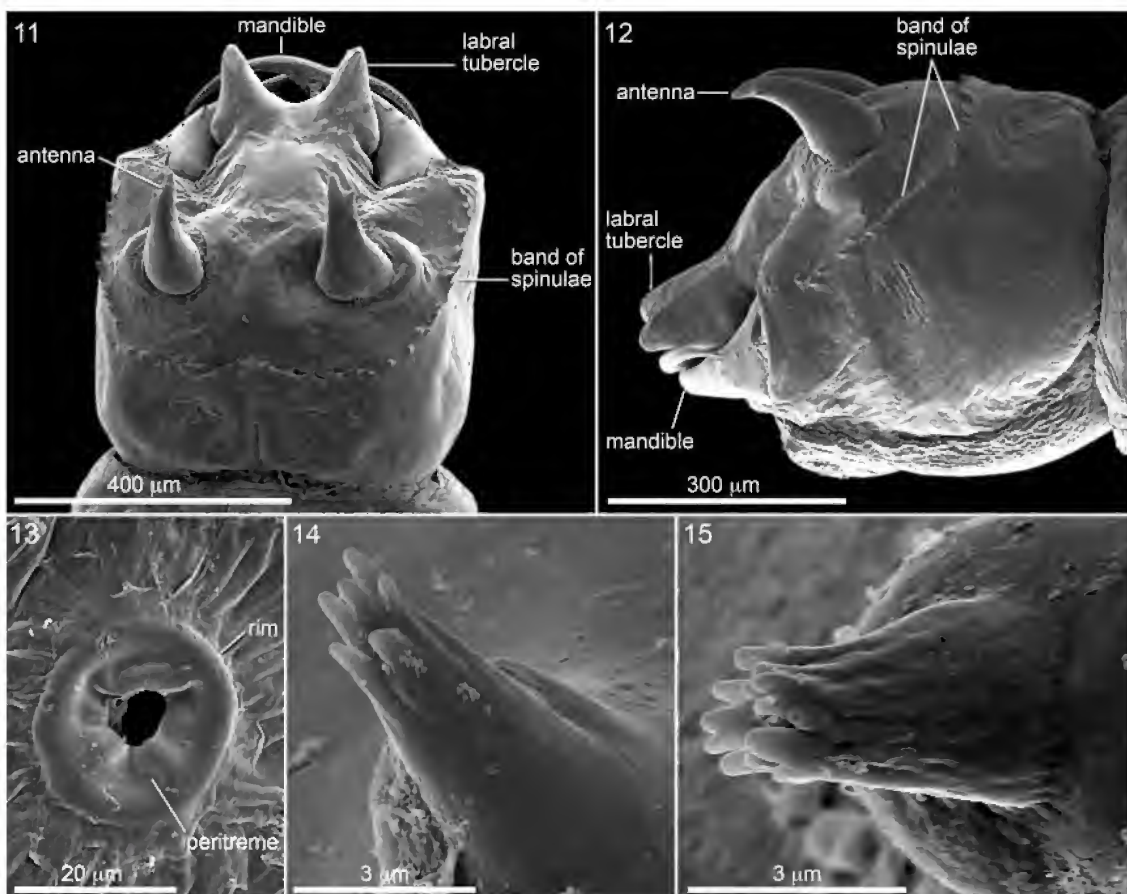
^bBased on collected eggs and average intertegular distance of collected females; ovaries not examined.

The largest oocyte was 2.46 mm long and 0.5 mm in maximum diameter. SEM examination of them was hampered by poor preservation, but showed that the micropyle consisted of a tight cluster of pores at the anterior end surrounded by pronounced radiating lines forming elongate polygons farther away from the clusters (figs. 8, 10). Thus, the chorionic ornamentation seems to closely resemble that shown for several species of *Melecta*, *Thyreomelecta kirghisia*, and *Xeromelecta californica* by Rozen and Özbek (2003: figs. 54–59, 62–65).

FIRST INSTAR

Figures 11–15

Giordani-Soika (1936) described the first instar of *Melecta* (s. str.) *luctuosa* (Scopoli), illustrated its head capsule, and compared it with first instars of *Sapyga* (Sapygidae) and *Chrysis* (Chrysididae). Torchio and Youssef (1968) described and fully illustrated first-instar *Zacosmia maculata*, and Torchio and Trostle (1986) and Bohart (1970) provided photographs of first instars of *Xeromelecta californica*. Rozen (1991) presented a tribal description of melectine first instars and comparative descriptions with illustrations of each of the following taxa: *Xeromelecta californica*, *Melecta separata callura*, *M. pacifica fulvida* Cresson, *Thyreus lieftincki*, and *Zacosmia maculata*. First-instar *Melecta duodecimmaculata* (figs. 11–15) is so similar to that of *Xeromelecta californica* (ibid.: figs. 14–22) that a separate description is unnecessary. The following diagnosis distinguishes it from all tribal taxa whose first instars have been described except for that of *X. californica*.



FIGURES 11–15. SEM micrographs of first instar of *Melecta duodecimmaculata*. 11, 12. Head, dorsal and lateral views, respectively. 13. Spiracle with raised rim and well-developed peritreme. 14, 15. Spinulae from head in figure 12 showing diversity of apical structures.

DIAGNOSIS: Head quadrate in dorsal view (fig. 11), with sides approximately parallel and width approximately equal to length measured from base of mandibles to posterior margin, as in *Xeromelecta californica* (Rozen, 1991: fig. 15) and unlike in *Melecta separata callura* (ibid.: fig. 24), *M. pacifica fulvida* (ibid.: fig. 30), *Thyreus lieftincki* (ibid.: fig. 34), and *Zacosmia maculata* (ibid.: fig. 38). Head in frontal view slightly wider than high measured from top of vertex to bottom of labium, but slightly higher than that of *Xeromelecta californica* (ibid.: fig. 17) and unlike those of *Melecta separata callura* and *Thyreus lieftincki* (ibid.: figs. 26, 31). Antenna moderately long in lateral view (fig. 12), as in *X. californica* (ibid.: fig. 18), not very long as in *M. separata callura* (ibid.: fig. 27) nor short as in *M. pacifica fulvida* (ibid.: fig. 32), *T. lieftincki* (ibid.: fig. 37), and *Z. maculata* (ibid.: fig. 41). Labral apex with tubercles moderately long, acutely pointed in dorsal outline (fig. 11), as in *X. californica* (ibid.: fig. 15), with tubercles not greatly elongate, as in *M. separata callura*, nor short (ibid.: fig. 29) and rounded (ibid.: figs. 34, 38), as in other species.

REMARKS: The linear band of spinulae⁶ (figs. 11, 12) that traverse the top of the head nearly from one anterior mandibular articulation to the other is a structure with an unknown function. Each spinula appears to rise from a broad base and to terminate in a sharp point, but its apex actually consists of a series of fine, apically rounded, parallel-directed projections. If these projections are sensory receptors, might the band function to tell the larva the tilt of its head relative to the liquid surface through which the larva navigates (fig. 6)? Alternatively (although not suggested by the description of egg hatching in *Xeromelecta californica*; Torchio and Trostle, 1986), if not sensory related, might these structures be instrumental for chorionic rupturing during eclosion?

LAST LARVAL INSTAR

The predefecating mature larva of *Melecta duodecimmaculata* is treated in Mature Larvae of the Melectini, below.

PUPA

Although pupae of *Melecta duodecimmaculata* were not recovered from the nesting site, we can reasonably predict that they, like known pupae of all Melectini (including that of *Thyreomelecta kirghisia*, described as *Thyreus* species? by Rozen, 2000), will have a pair of apically spine-bearing, mesoscutal tubercles (e.g., Rozen, 2000: figs. 17–20), a presumably unique feature of the tribe (Semi-chon, 1922; Porter, 1951; Cardale, 1968; Torchio and Youssef, 1968; Thorp, 1969; Rozen, 2000).

DISCUSSION

As pointed out in the section on Biology, above, the nesting biology of *Melecta duodecimmaculata* seems to differ little from that known about other Melectini.

⁶ The term “spinulae” for these structures was introduced by Torchio and Youssef (1968) in their description of first-instar *Zacosmia* (Melectini) and has been in use since then by others. If, however, these structures are found to have sensory perception, as suggested here, they should be renamed since spinulae (or spinules) by definition lack innervation (Nichols, 1989).

Does the information on biology and anatomy of immature stages help us understand the phylogenetic relationships of the Melectini within the family Apidae? As pointed out by Michener (2007), some past researchers have thought that the tribe arose from *Anthophora*, but he concluded on the basis of adult and larval characters that the tribe probably arose from an ancestor of *Anthophora* (Michener, 1953), as also concluded by Lieftinck (1959). From information presented in the appendix (below), the mature larvae of the Melectini are clearly different from known mature larval Anthophorini. Because representatives of only two of the seven anthophorine genera have been studied firsthand for this paper (larval *Habropoda miserabilis* [Cresson] had been described earlier by Torchio and Stephen, 1961), this matter needs to be revisited after more genera are studied. For the present, the known mature larvae of the Anthophorini and Melectini have substantially different mouthparts with respect to the labiomaxillary region and placement of the salivary opening. The mature larvae appear to share no specialized features that would suggest a close phylogenetic relationship between them, and the mature larvae of the Melectini do not show an affinity with other tribes of nonparasitic Apinae.

TABLE 2. List of anthophorine taxa the mature larvae of which were examined, arranged alphabetically by genus and subgenus, with sources of specimens, and references to previous descriptions, if any.

AMNH = American Museum of Natural History; KU = University of Kansas; UCB = University of California (Berkeley); UCD = University of California (Davis)

Taxon	Source	Reference
<i>Amegilla</i> (<i>Micramegilla</i>) <i>niveata</i> (Friese)	AMNH	
<i>Amegilla</i> (<i>Amegilla</i>) <i>salteri</i> (Cockerell)	KU	
<i>Anthophora</i> (<i>Anthophora</i>) <i>fulvitaris</i> Brullé	AMNH	
<i>Anthophora</i> (<i>Anthophora</i>) <i>melanognatha</i> Cockerell	AMNH	
<i>Anthophora</i> (<i>Anthophoroides</i>) <i>linsleyi</i> Timberlake	UCB	Michener, 1953
<i>Anthophora</i> (<i>Dasymegilla</i>) <i>muscaria</i> Fedtschenko?	AMNH	
<i>Anthophora</i> (<i>Heliophila</i>) <i>braunsiana</i> Friese	AMNH	
<i>Anthophora</i> (<i>Heliophila</i>) <i>rufolanata</i> Dours?	AMNH	
<i>Anthophora</i> (<i>Melea</i>) <i>abrupta</i> Say	AMNH (B. Norden)	
<i>Anthophora</i> (<i>Melea</i>) <i>bomboides</i> Kirby	KU, UCB	Michener, 1953 (As <i>A. stanfordiana</i>)
<i>Anthophora</i> (<i>Melea</i>) <i>occidentalis</i> Cresson	AMNH	
<i>Anthophora</i> (<i>Melea</i>) <i>plagiata</i> (Illiger)	AMNH	
<i>Anthophora</i> (<i>Mystacanthophora</i>) <i>arequipensis</i> Brèthes	AMNH	
<i>Anthophora</i> (<i>Mystacanthophora</i>) <i>paranensis</i> Holmberg	AMNH (F. Vivallo)	
<i>Anthophora</i> (<i>Mystacanthophora</i>) <i>tricolor</i> (Fabricius)	AMNH (F.D. Bennett)	
<i>Anthophora</i> (<i>Petalosternon</i>) <i>albifascies</i> Alfken	AMNH	
<i>Anthophora</i> (<i>Pyganthophora</i>) <i>edwardsii</i> Cresson	UCB, UCD	Michener, 1953; Thorp, 1969
<i>Habropoda miserabilis</i> (Cresson) [species considered based on published description; not examined first hand]	P.H. Torchio and W.P. Stephen, 1961	

Recently, Cardinal et al. (2010) produced a molecular phylogeny of the Apidae indicating that cleptoparasitism evolved *de novo* only four times in the family, once each for *Ctenoplectrina*, *Aglae*, *Exaerete*, and all others. Thus, the Nomadinae, Ericrocidini, Rhathymini, Isepeolini, Protepeolini, Osirini, *Coelioxoides*, and Melectini appeared as a monophyletic clade. Within this clade, there were two basic monophyletic groups; one consisted of Ericrocidini, Rhathymini, Isepeolini, Protepeolini, Osirini, and *Coelioxoides* and the other of the Nomadinae plus the Melectini as their sister taxon.

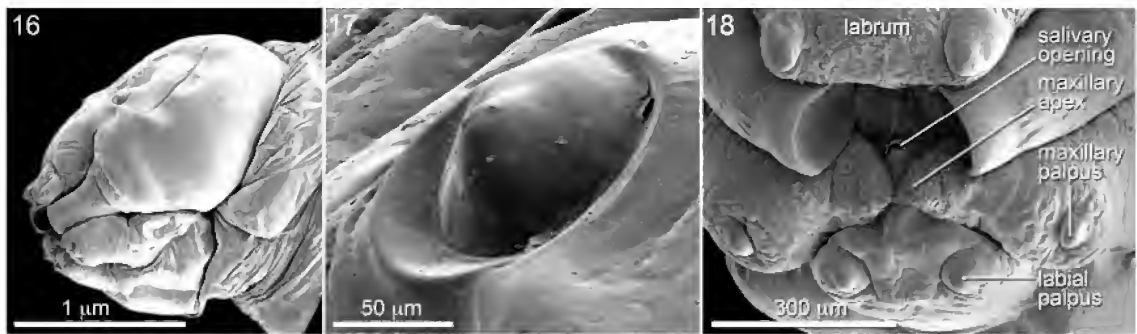
Previous studies of adult and larval anatomy had affirmed the monophyly of the Nomadinae (Roig-Alsina and Michener, 1993) as had others based on their biology and mature larvae (e.g., Rozen, 1996, 2003). However, none of these studies, including ones based on first instar morphology and modes of cleptoparasitism (Rozen, 1991; Rozen et al., 2006: table 2), demonstrate convincing evidence indicating phylogenetic ties among the other cleptoparasitic Apinae. The bootstrap value of the large parasitic clade of Cardinal et al. (2010) is very low; this clade is well supported only under model-based analysis. These facts suggest the need for future studies.

In the current study, the Melectini share a variety of features with other parasitic groups within the Apidae regarding larval behavior and first-instar anatomy. Rozen et al. (2006; table 2) presented a table that compared attributes associated with mode of cleptoparasitism of eight lineages of noncorbiculate bees belonging to the Apinae. One of the eye-catching similarities is the fact that both *Mesoplia* (Ericrocidini) and the Melectini introduce their eggs into closed host cells through small circular openings (about the diameter of an egg) in closures of vertical host cells. Eggs are affixed, usually by one end to the undersurfaces of the closures, usually a short distance from the entrance hole. With both taxa the egg hatches into a larva with sharp-pointed mandibles with which the first instar kills the host egg. No other parasitic bee taxa hang their eggs by one end to the roof of vertical cells,⁷ so that at first glance this discovery suggests a striking synapomorphy between the two tribes (assuming, of course, that unstudied contribal relatives will be found to have features similar to those that have been studied).

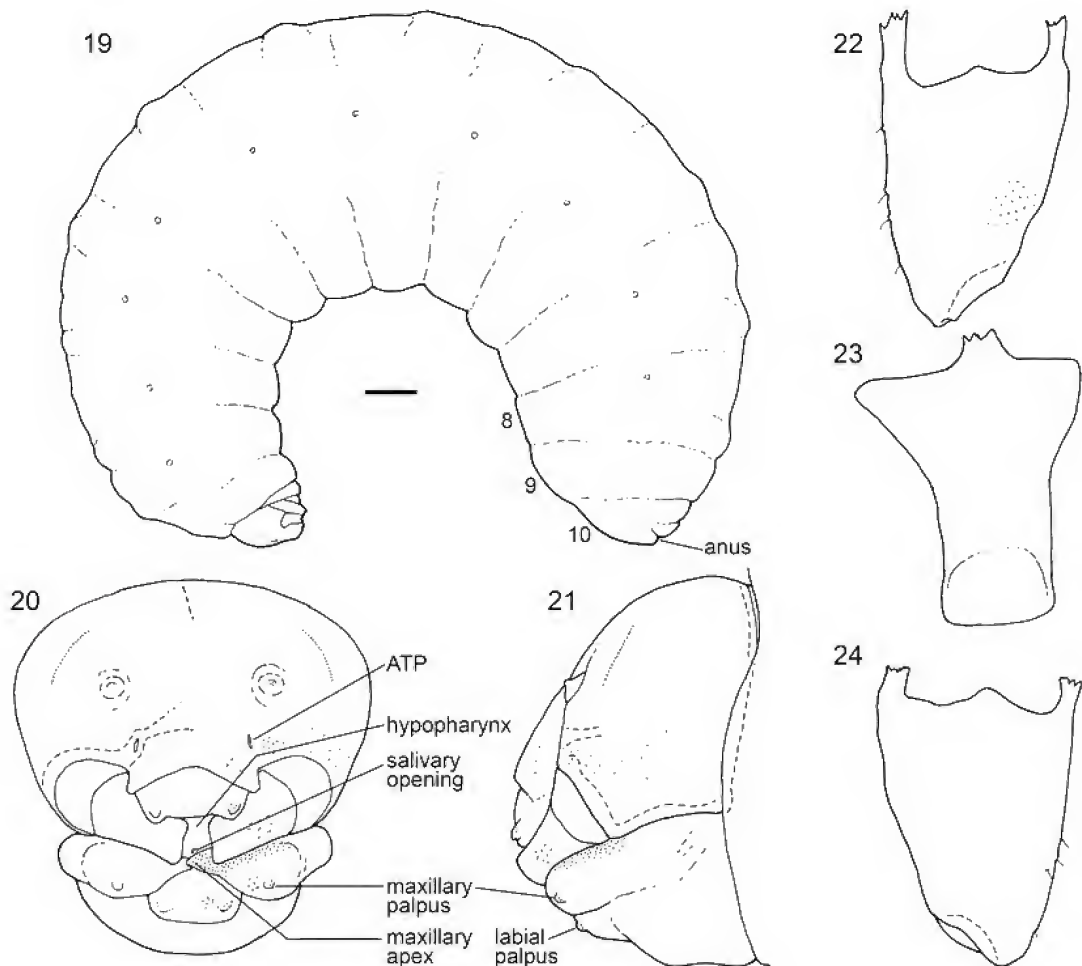
There is one major difference between these two tribes with respect to egg deposition: the eggs of Melectini are attached by their posterior ends to the cell closure, and those of the *Mesoplia* and presumably other Ericrocidini are attached by their anterior ends. This implies that ovipositing females must use different behavioral gymnastics in affixing their eggs since all bee eggs are deposited with the posterior part of their eggs emerging first from the common oviduct. We have no information as to how the eggs are deposited with either group, but egg manipulations must be different, suggesting the potential synapomorphy may be flawed, arguing against homology.

Furthermore, we do have some insight into major differences in eclosion and posteclosion behavior. A recent study (Rozen et al., 2011) of *Mesoplia* (s. str.) *sapphirina* Melo and Rocha-Filho presented a detailed description of its egg and highlighted a remarkable but unexplained change in shape during late embryogenesis (compare *ibid.*: figs. 14, 21 with *ibid.*: fig. 29). The anterior end of the egg, no longer than the diameter of the egg at midlength, swells and its apex

⁷ Camargo et al. (1975) assumed that the egg of an unknown species of *Rhathymus* (Rhathymini) was inserted through the cell closure and attached to its inner surface, but that was not certainly known and the cells were presumed to be horizontal in most cases.



FIGURES 16–18. SEM micrographs of larval head of mature larva of *Anthophora melanognatha*. 16, 17. Entire head and close-up of antenna showing few sensilla, approximate lateral view. 18. Mouthparts of same, frontal view.



FIGURES 19–24. Diagrams of last larval instar of *Anthophora melanognatha*. 19. Entire larva, lateral view. 20, 21. Head, frontal and lateral views, respectively. ATP = anterior tentorial pit. 22–24. Right mandible, dorsal, inner, and ventral views, respectively.

invaginates (ibid.: figs. 29, 36). We now hypothesize that the swelling and invagination of the front end of the *Mesoplia* egg may be the mechanism whereby the egg is released from its attachment: perhaps during the invagination, the point of attachment separates while the rim of the invagination pushes against the cell closure. Once the egg is separated from the closure, it drops onto the provisions, and there the first instar somehow destroys the front of the chorion, emerges partway, and crawls about with the empty chorion attached to its terminal abdominal segments (Rozen et al., 2011: figs. 24–28, 38).⁸

In contrast, first instars of melectines emerge from eggs that stay attached by their posterior ends as the larvae slip out (Torchio and Trostle, 1986: figs. 6–13). There has been no indication of a late embryonic change in the front end of the egg, and the first instar does not crawl about with its chorion attached. A coarser chorionic sculpturing of the extreme rear of their eggs and a smoother surface elsewhere (Rozen and Özbek, 2003: figs. 55, 63) as well as a more rounded rear contour (ibid.: fig. 63) may be adaptations providing additional adhesive surface for gluing melectine eggs to the closure; compare them to the more pointed, uniformly sculptured rear of the *Mesoplia* egg (Rozen, 2003: fig. 48).

If these hypotheses are supported by future investigation, a seemingly conspicuous synapomorphy must be rethought, perhaps as follows: cleptoparasitic Apinae (as well as all cleptoparasitic bees) must introduce their eggs into host brood cells by hiding them in cells that are still open (Nomadinae, Protepeolini, Isepeolini) or by opening cells that have already been closed by the host female (Melectini, Rhathymini, Ericrocidini, *Coelioxoides*, *Protosiris*, *Exaerete*⁹). Among the last group, eggs are introduced through small (Melectini, Rhathymini?, Ericrocidini) or large (*Coelioxoides*) holes, presumably with the tip of their metasomas. Others (*Protosiris*, Rozen et al., 2006, and *Exaerete*, Bennett, 1972; Garófalo and Rozen, 2001) make a large opening with their mandibles and through that opening they kill or remove the host egg, oviposit, and then close the opening. Hence, inserting eggs into a cell through a small hole is simply one of numerous ways for a cleptoparasite to introduce her egg into a cell.

APPENDIX: TRIBAL DESCRIPTIONS OF THE ANTHOPHORINI AND MELECTINI BASED ON THEIR MATURE LARVAE

Because bee larvae are becoming better known through expanding collections and published descriptions, it is now possible to learn the extent to which larval characters can define higher taxa. For this reason several papers have recently been produced on larvae of the Apidae that provide tribal descriptions of their mature larvae, exclusive of the parasitic and corbiculate taxa: Exomalopsini (Rozen, 2011a) and Emphorini (Rozen, 2011b). Although no tribal descrip-

⁸The invariable occurrence of this feature in this species and in a related one and the modified posterior tip of the first instar's abdomen (ibid.: fig. 43) suggests that the lack of complete separation is not an accident of eclosion but is actually functional.

⁹Though a corbiculate, *Exaerete* is included here because it is an Apinae, and there is information about its mode of parasitism. However, it is distantly related to the other cleptoparasitic tribes under discussion since its first instar is not hospicidal whereas its second instar seems to be, at least in the case of one species (Garófalo and Rozen, 2001).

tion of other tribes have been drafted, the following are the most recent papers on larvae of other tribes that would serve well as the basis for tribal presentations: Ctenoplectrini (Rozen, 2010), Tapinotaspidiini (Rozen et al., 2006), and Tetrapediini (Alves dos Santos et al., 2002).

MATURE LARVAE OF THE ANTHOPHORINI

Figures 16–25, 28

DIAGNOSIS: Mature anthophorine larvae display a set of strong characters that set them apart from immatures of other nonparasitic, long-tongued bees. In addition to their robust body form (fig. 19), they do not spin cocoons and therefore lack broad, projecting salivary lips. Although larvae of a number of tribes have the maxillary palpus subapically positioned relative to a somewhat adorally projecting inner apical angle of the distal region, the length of this spiculate projection in the Anthophorini is unsurpassed (figs. 18, 20, 28) among other larval Apidae. Furthermore, the salivary gland opening tends to be far removed from the labial palpi as seen in frontal view (figs. 18, 20, 28) and recessed above and posterior to the labial apex, as is also true for *Tetrapedia* (Tetrapediini), but the mandible of the latter is apically bidentate (Alves-dos-Santos et al., 2002: figs. 17–19) unlike that of most Anthophorini (figs. 22–24). Although Torchio and Stephen (1961: fig. 5a–c) depict a bidentate mandible of *Habropoda miserabilis*, they also picture its spiracle (ibid.: fig. 5a, b) with a massively spined primary tracheal opening, as characteristic of other anthophorines, unlike the simple opening of *Tetrapedia* (Alves-dos-Santos et al., 2002: fig. 47). The anthophorine maxillary and labial palpi (figs. 18, 21) are coequal in size, their lengths less than their basal diameters, as is also the case for *Epicharis* (Centridini) (Rozen, 1965: figs. 63, 64, 72), but the apically broad, scoop-shaped anthophorine mandible is usually composed of a single apical tooth rather than being apically bilobed as in centridines (ibid.: figs. 41, 47, 50, 59, 67, 70). In the Anthophorini the atrial wall is ornamented with a reticulated pattern of concentric lines that on most species are more or less spiculate especially near the primary tracheal opening. Although larvae of some other bees have spiculate, patterned atrial walls, the primary spiracular opening guarded by long, concentrically pointing spines is found only in the Anthophorini (fig. 25), some *Bombus* (Bombini) (Michener, 1953), some (or all) *Acanthopus*, *Mesoplia* (Ericrocidini) (Rozen, 1969b: figs. 48, 53; Rozen et al., 2011), as well as in *Epicharis* (Centridini) (Rozen, 1965: fig. 65; Camargo et al., 1975: figs. 6G, H). These spines presumably exclude pollen and perhaps soil and parasites from entering tracheal systems.

Thus mature larvae of all taxa identified in table 3 will key out successfully in the Preliminary Tribal Key to Mature Larvae of Nonparasitic Apinae Exclusive of the Corbiculate Tribes (Rozen, 2011a).

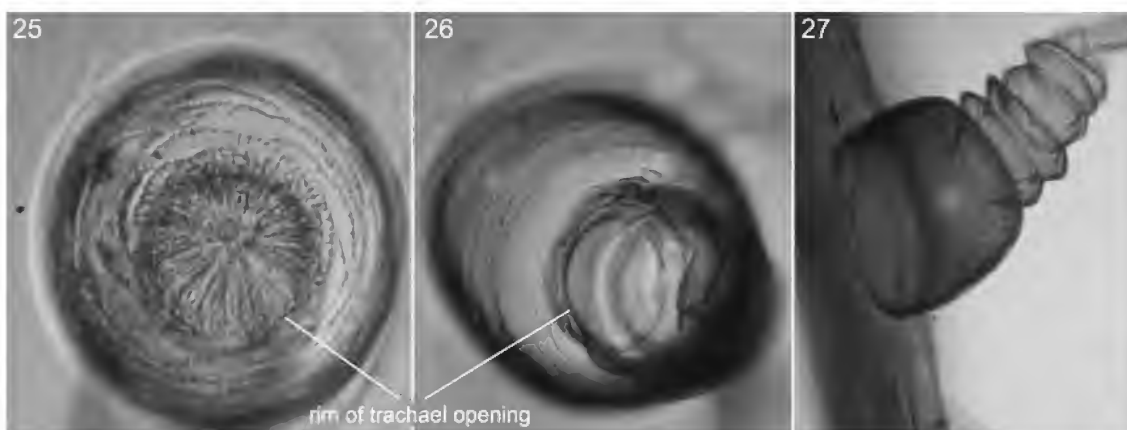
Mature anthophorine larvae are easily distinguished from those of the Melectini, which have a much longer antennal papilla (about as long as basal diameter) as well as a recessed maxillary apex relative to the labial apex in lateral view (figs. 30, 32, 37) (even in the case of *Thyreus*, which does not spin a cocoon, Rozen, 1969a: fig. 19). In contrast, the anthophorine antennal papilla is extremely low (figs. 16, 17) and the maxillary apex projects as far as, if not

farther than, that of the labium in lateral view (figs. 18, 20, 28) and bears a uniquely elongate, spiculate, tuberclelike, inner apical projection that can often meet or overlap the same projection of the opposite maxillary apex (figs. 18, 20, 28).

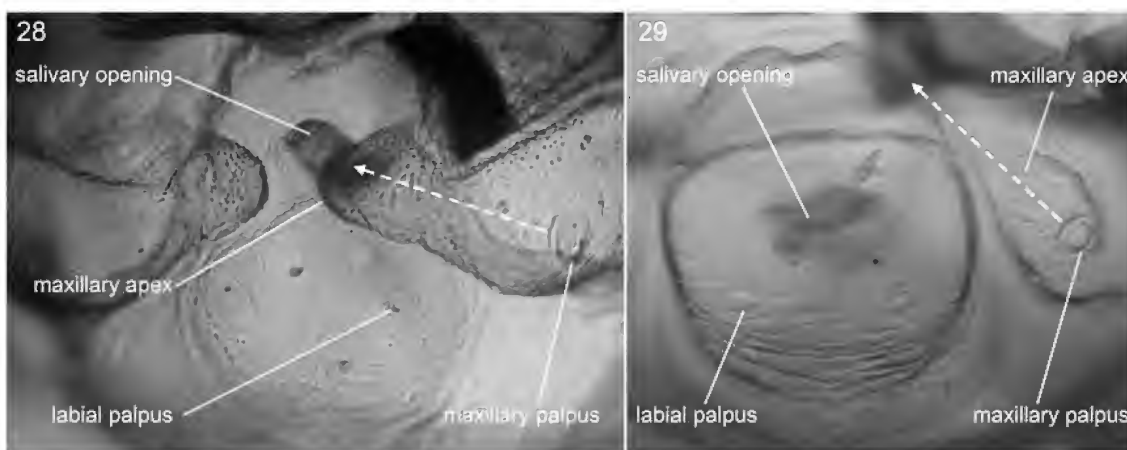
DESCRIPTION: Head: Integument of head capsule with scattered, minute sensilla, so small as not to appear setiform under stereomicroscope; epipharyngeal surface without spicules medially but with patch of short spicules laterally behind base of each lateral tubercle; mandibular corium nonspiculate. Integument unpigmented except for mandibular apices but faintly pigmented at mandibular points of articulation with head capsule.

Head moderately small compared to robust body (fig. 18); width of foramen magnum compared to head width 0.79–0.88; tentorium well developed, especially for noncocoon-spinning larva. Center of anterior tentorial pit only slightly closer, to distinctly closer, to anterior mandibular articulation than to outer ring of antenna in frontal view (fig. 20); posterior tentorial pit (i.e., junction point of postoccipital ridge, hypostomal ridge, and tentorial bridge) in normal position, moderately recessed; all internal ridges tending to be well developed; coronal ridge fading about halfway from vertex to level of antennae in frontal view; dorsomedial portion of postoccipital ridge straight or nearly so (not bending forward) as viewed from above; hypostomal ridge without distinct dorsal ramus. Parietal bands evident as integumental scars. Antennal prominence scarcely extant; length of antennal papilla low, about one-half basal diameter. Apex of labrum (figs. 18, 20) subtruncate in frontal view; with paired, downward-projecting, sensilla-bearing tubercles at extreme lateral corners; transverse labral sclerite absent.

Mandible short, as seen from above or below (figs. 22, 24), robust at base, gradually tapering to apex, which bears large, darkly pigmented, scoop-shaped apical concavity; mandible as seen in inner or outer view tapering very gradually toward apex, so that apex ends in single (except for *Habropoda miserabilis*), broad, curved, truncate edge (figs. 23) lacking teeth; cusp not defined; apical concavity large, scoop shaped, adorally directed; dorsal mandibular surface often with cluster of a few small spicules (fig. 22); outer mandibular surface with approximately 2 (*A. muscaria*?) to 8 (*A. melanognatha*) short, inconspicuous setae, sometimes on small tubercles. Labiomaxillary region often large in lateral view (figs. 16, 21). Maxilla tending to project as far as, or farther than, labium in lateral view; inner lobe of maxillary apex in frontal view (figs. 18, 20, 28) greatly produced as large apically spiculate tubercle, apex of which is only slightly above level of palpal base, so that line drawn from palpal base to apex of inner lobe points toward opposite palpus well below oral opening; distance between palpal base (cf. description of maxillary apex of Melectini) and lobe apex inordinately long (figs. 18, 20, 28), so that apices of opposing maxillae sometimes overlapping. Maxilla with apex turned adorally, bearing palpus subapically; additionally, apex projecting farther as large, apically rounded, spiculate, adorally directed tubercle; galea presumably represented by cluster of approximately 3–6 sensilla short distance mesad of maxillary palpus but not on elevated projection; cardo and stipes scarcely sclerotized, unpigmented; articulating arm of stipital sclerite not evident; maxillary palpus evident as small papilla somewhat shorter than basal diameter. Labium divided into small prementum and large postmentum; premental sclerite not evident; labial palpus small, about equal in size to maxillary palpus. Salivary opening transverse, without projecting lips,



FIGURES 25, 26. Microphotographs of spiracles of cleared mature larvae, showing ornamentation of atrial walls and primary tracheal openings. **25.** *Anthophora melanognatha*. **26.** *Melecta duodecimmaculata*. FIGURE 27. Microphotograph of spiracle of *Melecta duodecimmaculata*, approximate side view.



FIGURES 28, 29. Microphotographs of cleared mouthparts, right mandible removed, showing left maxilla and labium, approximate frontal view; for explanation of arrows, see text. **28.** *Anthophora melanognatha*. **29.** *Melecta duodecimmaculata*.

positioned behind labial apex, immediately distad of hypopharyngeal groove on prementum and far from labial palpi. Hypopharynx paired spiculate lobes behind hypopharyngeal groove.

Body: Integument without general body setae; ventral surfaces weakly spiculate. Body form of pre- and postdefecating larva large, robust; most body segments divided dorsally into cephalic and caudal annulets; intersegmental lines moderately impressed; intrasegmental line weakly so; paired dorsal tubercles on caudal annulets more or less faintly elevated, with those of thoracic segments transverse, faintly sclerotized (best observed on stained specimen) and those of following segments sometimes also faintly sclerotized depending on taxon; abdominal segment 9 on pre- and postdefecating forms produced ventrally compared with following segment, so that segment 10 positioned dorsally on segment 9 in lateral view (fig. 19); anus posi-

TABLE 3. List of melectine taxa whose mature larvae were examined, with sources of specimens examined and references to previous descriptions, if any.

AMNH = American Museum of Natural History; KU = University of Kansas; UCD = University of California (Davis)

Taxon	Source	Reference
<i>Melecta</i> (<i>Melecta</i>) <i>duodecimmaculata</i> (Rossi)	AMNH	
<i>Melecta</i> (<i>Melecta</i>) <i>separata</i> Cresson	UCD	Thorp, 1969
<i>Thyreomelecta kirghisia</i> Rightmyer & Engel	AMNH	
<i>Thyreus lieftincki</i> Rozen	AMNH	Rozen, 1969b
<i>Thyreus</i> sp. (Australia)	KU	Rozen, 1969b
<i>Xeromelecta</i> (<i>Melectomorpha</i>) <i>californica</i> (Cresson)	AMNH	Michener, 1953
<i>Zacosmia maculata</i> (Cresson)	AMNH	Torchio and Youssef, 1968; Rozen, 1969b

tioned close to dorsal surface on segment 10 (fig. 19); on postdefecating larvae, dorsal surface of segment 10 traversed by groove extending from one side of anus to other side and forming strong transverse ridge posteriad to it that surrounds anus dorsally. Spiracles (fig. 19) moderately small, inconspicuous, subequal in size throughout, not surrounded by sclerites, and not on tubercles; peritreme present, in some species spiculate; atrium projecting beyond body wall, with distinct rim, globose; atrial wall patterned with lines forming elongate polygons concentric with primary tracheal opening (fig. 25) in all species examined; borders of polygons varying from fine lines to rows of spicules (fig. 25) although lines closest to primary tracheal opening always spiculate; tracheal opening in all species guarded by large, concentrically directed spines, subatrium varying from normal in length, consisting of about 12 chambers, to short, consisting of 4 chambers, depending on species; subatrial chambers somewhat decreasing in outside diameter from body surface inward. Males, to extent known, with single median scar on ventral protuberance of abdominal segment 9; females presumably lacking scars.

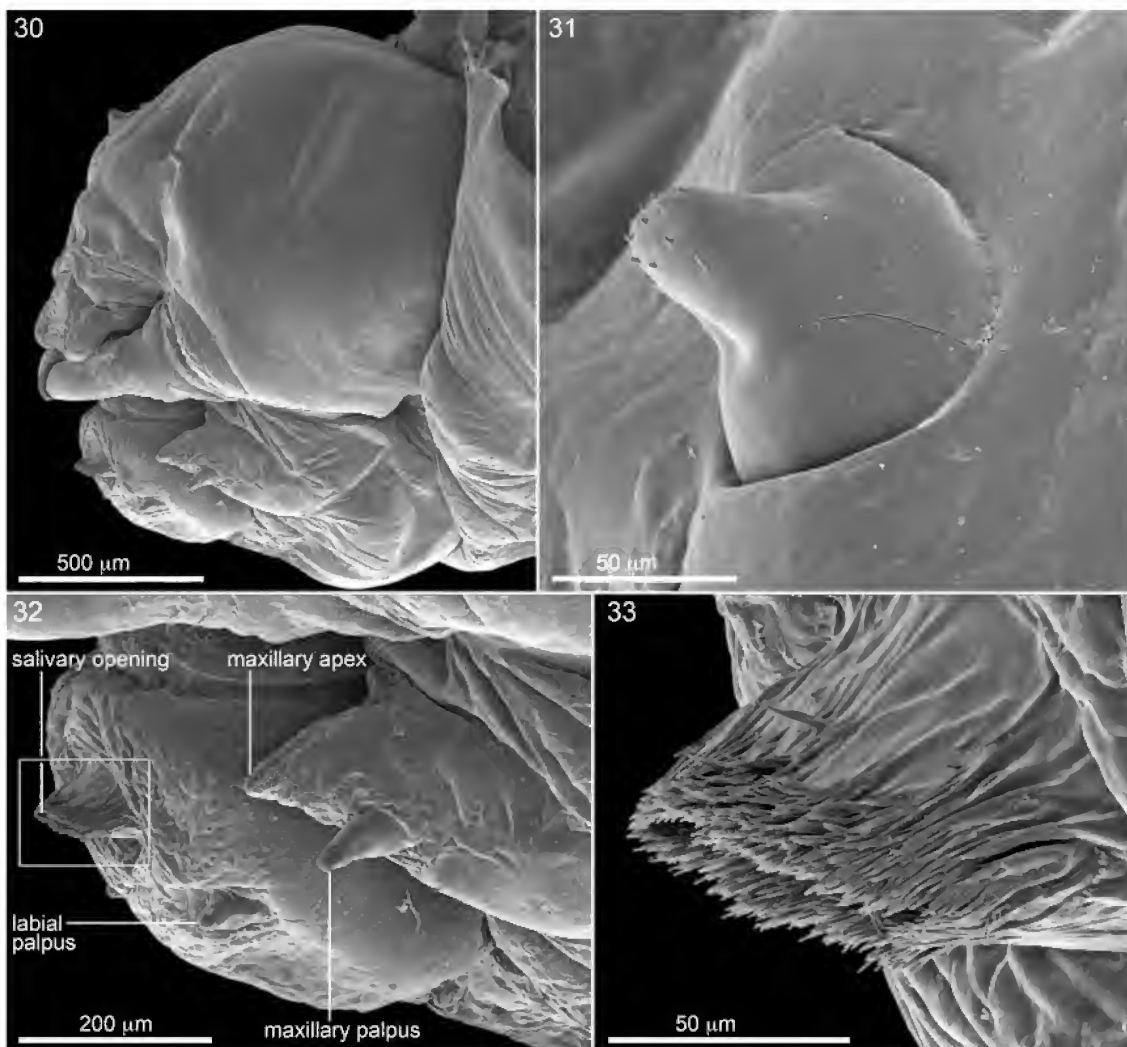
MATERIAL STUDIED: The above tribal description was based primarily on the species listed in table 2.

REMARKS: Semichon (1925) initially the distinctive primary tracheal opening of an anthophorine (*Anthophora fulvitaris*) to be different from that of its melectine parasite (*Melecta albifrons*).

MATURE LARVAE OF THE MELECTINI

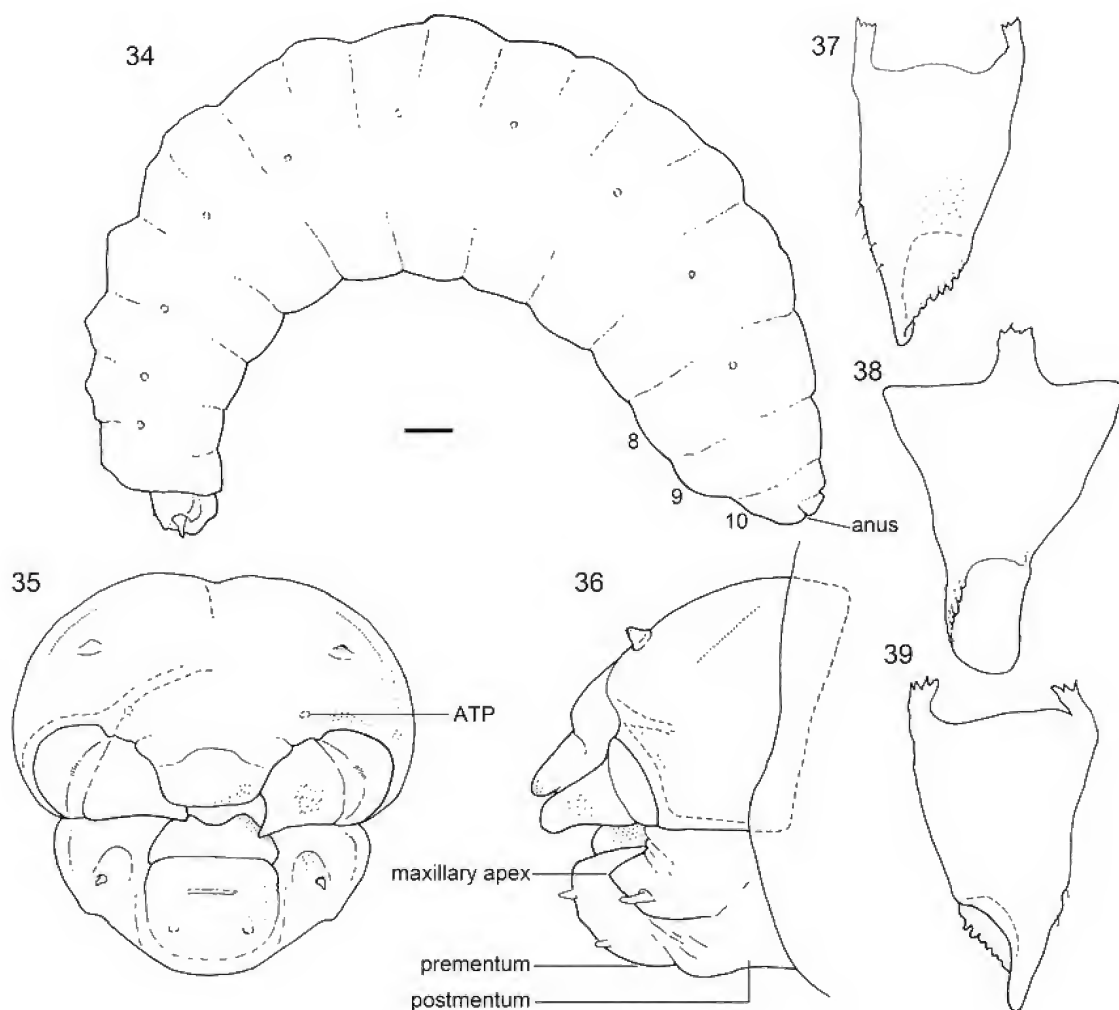
Figures 26, 27, 29–50

DIAGNOSIS: In addition to the features separating melectine mature larvae listed in the diagnosis of the Anthophorini above, these larvae have a uniquely short maxilla in relation to the labium, all as seen in lateral view (figs. 30, 32, 36, 43–45, 48); Michener, 1953: fig. 238). The following key to available mature larvae of melectines provides insight into intratribal variation based primarily on mandibular morphology.¹⁰

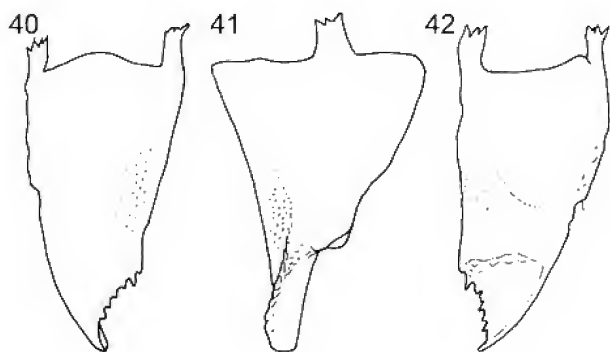


FIGURES 30–33. SEM micrographs of head and antenna of mature larva of *Melecta duodecimmaculata*, semi-lateral view. **30.** Entire head. **31.** Antenna and close-up of apex showing abundant sensillae, respectively. **32.** Labiomaxillary apex. **33.** Close-up of salivary opening from figure 32, showing apical brushlike filament.

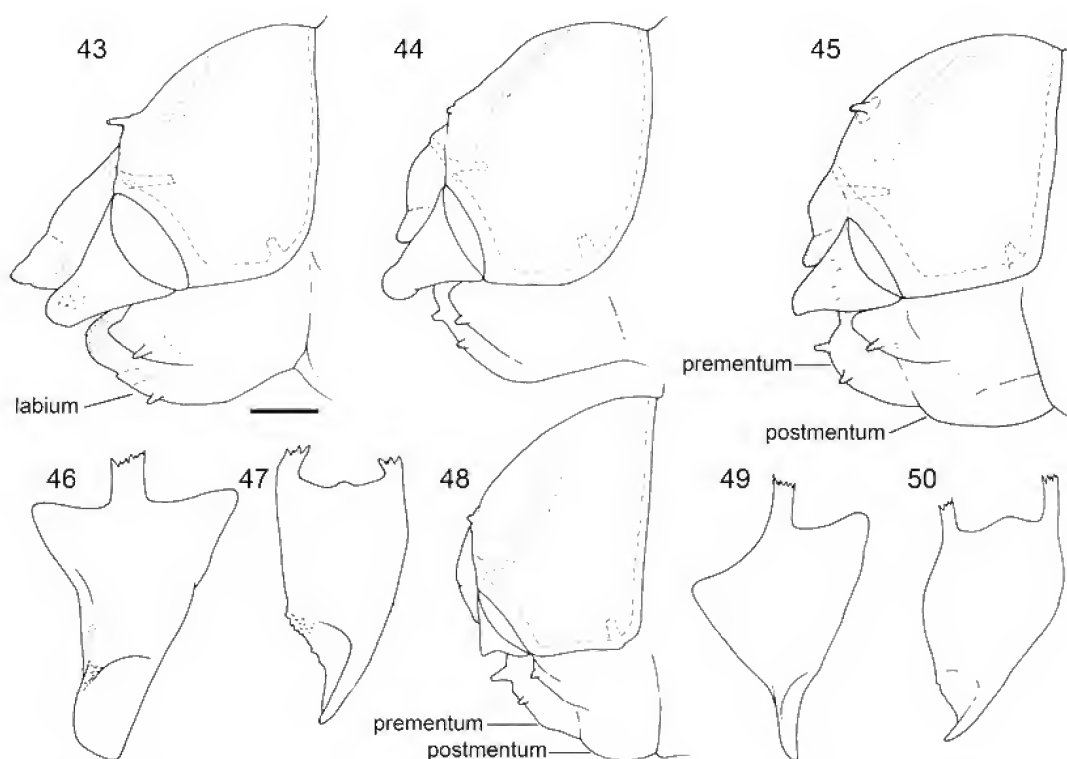
10 In addition to the taxa whose larvae are treated in the key, the last larval skin of *Thyreomelecta kirghisia* Rightmyer and Engel was collected with the pupa in Kyrgystan: Issyka-kul, 10 km E of Kadzhi-Saj, VII-5-1999 (J.G. Rozen). Although many of its features are distorted, so it can not be included in the key, certain features are of interest. The antennal papilla is large and as long as its basal diameter, typical of those of other melectines. Spiracles are moderately large, have walls with concentric rows of fine spicules, and in general conform to the shape of those of other melectine larvae. The mandible is apically pointed, heavily sclerotized, and pigmented, but its apex curves inward, and tapers to an acute point. Thus, it appears more fanglike than those of other known taxa. Its dorsal apical edge is crenulate, as if the teeth have become more evenly and smoothly curved than those of other related taxa. Although the pupa was not enclosed in a cocoon when collected, we cannot determine from the distorted larval skin whether the larval labium was undivided or divided into a prementum and postmentum.



FIGURES 34-39. Diagrams of last larval instar of *Melecta duodecimmaculata*. 34. Entire larva, lateral view. 35, 36. Head, frontal and lateral view, respectively. ATP = anterior tentorial pit. 37-39. Right mandible, dorsal, inner, and ventral views, respectively.



FIGURES 40-42. Right mandible of *Xeromelecta californica*, dorsal, inner, and ventral views, respectively.



FIGURES 43–50. Diagrams of heads, lateral view, and mandibles of mature melectine larvae. **43.** *Thyreus lieftincki*. **44.** *Thyreus* sp. **45–47.** *Melecta separata callura*, and right mandible, inner and ventral views, respectively. **48–50.** *Zacosmia maculata*, head and right mandible, inner and ventral views, respectively.

1. Labium not divided into prementum and postmentum (noncocoon spinners) (figs. 43, 44)
 - *Thyreus lieftincki* Rozen; *Thyreus* sp.
 - Labium divided into prementum and postmentum (figs. 36, 45, 48) (cocoon spinners) ... 2
- 2(1). Mandibular apex narrow, acutely pointed in inner view (fig. 49); dorsal apical edge slightly irregular but completely lacking teeth in ventral view (i.e., nondentate) (fig. 50) .
 - *Zacosmia maculata* (Cresson)
 - Mandibular apex usually much broader, rounded to subtruncate in inner view (figs. 38, 46) but if somewhat narrow (as in *Xeromelecta californica*, fig. 41), then dorsal apical edge of mandible clearly dentate in ventral view (fig. 42) 3
- 3(2). Dorsal apical edge of mandible with teeth restricted to base of apical concavity as seen in ventral view (fig. 47); mandibular apex broad as seen in inner view (fig. 46)
 - *Melecta separata callura* (Cockerell)
 - Dorsal apical edge of mandible with teeth larger, along entire edge as seen in ventral view (figs. 39, 42); mandibular apex broad or narrow 4
- 4(3). Mandibular apex broad as seen in inner view (fig. 38); outer edge of apex straight in ventral view (fig. 39) not curving adorally *Melecta duodecimmaculata* (Rossi)
 - Mandibular apex narrow in inner view (fig. 41); outer edge of apex in ventral view (fig. 42) curved adorally. *Xeromelecta californica* (Cockerell)

DESCRIPTION: Head: Integument of head capsule with scattered small sensilla that are clearly setiform under stereomicroscope; epipharyngeal surface with patch of weak spicules behind base of each lateral tubercle; mandibular corium nonspiculate. Integument unpigmented except for mandibular apices but faintly pigmented at mandibular points of articulation with head capsule.

Head moderately small compared to robust body (fig. 34); maximum width of foramen magnum compared to maximum head width 0.8; tentorium well developed. Center of anterior tentorial pit distinctly closer to anterior mandibular articulation than to outer ring of antenna in frontal view (fig. 35); posterior tentorial pit (i.e., junction point of postoccipital ridge, hypostomal ridge, and tentorial bridge) in normal position, moderately recessed; all internal head ridges tending to be well developed; coronal ridge fading about halfway from vertex to level of antennae in frontal view; dorsomedial portion of postoccipital ridge straight (not bending forward) as viewed from above; hypostomal ridge with distinct dorsal ramus, which is so short that it is not apparent in side view. Parietal bands faintly evident as integumental scars. Antennal prominence scarcely extant; antennal papilla projecting, with length about equal to basal diameter. Apex of labrum (fig. 35) at most faintly bilobed in frontal view because of pair of low sensilla-bearing tubercles on outer surface; transverse labral sclerite absent.

Mandible moderate in length, as seen from above or below (figs. 37, 39), robust at base, gradually tapering to sclerotized apex, where moderately large, adorally directed, scoop-shaped apical concavity begins; mandible in inner or outer views (fig. 38) tapering to apical concavity that is longer than broad and distally ends in single apex (fig. 38); dorsal apical edge of concavity transversely curved in inner view, often with fine, more or less even teeth, but on some species teeth reduced, found only near base of apical concavity or completely absent; ventral apical edge nearly straight, lacking teeth; cusp not defined; dorsal mandibular surface often with cluster of fine spicules (figs. 37, 40, 46); outer mandibular surface with as many as 8 moderately small setae, sometimes on small tubercles. Labiomaxillary region often large, but maxilla extremely short in lateral view (figs. 36, 43–45, 48). In lateral view, maxillary apex ending well behind labium and hypopharynx; in frontal view, inner lobe of maxillary apex (figs. 29, 32, 35) well above level of palpus, so that imaginary line, drawn from palpal base to apex of inner lobe, points to oral opening (see figs. 28, 29: dashed arrows); inner lobe not greatly enlarged, so that distance from palpal base of lobe apex short; cardo and stipes scarcely sclerotized, unpigmented; articulating arm of stipital sclerite not evident; maxillary palpus stout, tapering, length three times basal diameter. Labium clearly divided into prementum and postmentum in *Melecta*, *Zacosmia*, *Xeromelecta*, but not in *Thyreus* (condition in *Thyreomelecta* uncertain); premental sclerite not evident; labial palpus smaller than maxillary palpus, length nearly two times basal diameter. Salivary opening transverse, with projecting lips, those of *M. duodecimmaculata* with apical brushlike filaments (fig. 33), positioned on labial apex well before hypopharyngeal groove. Hypopharynx represented by paired spiculate lobes behind hypopharyngeal groove.

Body: Integument without general body setae; ventral surfaces very finely spiculate. Body form of predefecating larva large, tapering posteriorly (fig. 34); most body segments divided dorsally into cephalic and caudal annulets; intersegmental lines moderately weakly impressed

but variable depending on preservation; intrasegmental line weakly so; paired dorsal tubercles on thoracic segment faintly elevated but on cleared, stained specimen evident as faint transverse sclerites; abdominal segments without distinct paired dorsal tubercles, but caudal annulet tending to be slightly more elevated than cephalic annulet and in some cases faintly sclerotized on cleared specimens; abdominal segment 9 on pre- and postdefecating forms produced ventrally compared with following segment, so that segment 10 positioned dorsally on segment 9 in lateral view (fig. 34); anus positioned close to dorsal surface on segment 10 (fig. 34); on cleared, stained specimen abdominal segment 10 of predefecating larva with sclerite arching over anus; on postdefecating larva area between anus and sclerite becoming planar and posterior edge of sclerite forming ridge, so that dorsal surface of segment 10 traversed by groove extending from one side of anus to other side. Spiracles (figs. 26, 27, 34) moderately large, subequal in size throughout, not surrounded by sclerites, and not on tubercles; peritreme present; atrium projecting beyond body wall, with distinct rim, globose; atrial wall with fine to obscure spicules, more or less in linear series arranged concentrically with primary tracheal opening; atrial wall without distinct lines as in Anthophorini; primary tracheal opening without spines, subatrium tending to be short, consisting of about 4–8 chambers (fig. 27): subatrial chambers somewhat decreasing in outside diameter from body surface inward. Sex characters unknown.

MATERIAL STUDIED: Table 3 lists the species whose larvae were examined first hand in developing this tribal description.

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